PUCCINIASTRUM ON EPILOBIUM AND ABIES

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Approximately 40 species of *Epilobium* are recorded among the hosts that are susceptible to infection from rust fungi of the genus *Pucciniastrum*. Persoon (15) cited the first one in 1801 when he described *Uredo pustulata* n. sp. on *Epilobium montanum* L. Various other mycologists have had a share in making up the rest of the list. Turning from the impressive list of host plants to the rusts involved we find that little progress has been made towards a delineation of their specific characters if they comprise more than one species, an elucidation of their life histories, a determination of their host restrictions or an appraisal of their economic importance. These desiderata can be realized only through experimentation. This is true even with reference to the taxonomic considerations because, with one exception, the diploid phase alone is known and that phase presents little morphological diversity, one form compared with another.

With respect to previous experimental work on the Pucciniastrum-Epilobium rusts, the few investigations so far published have been almost solely restricted to life-history studies of the form on *E. angustifolium* L. Klebahn (9–13) was the first to demonstrate that this has its haploid phase on *Abies* and that it is limited in its choice of Epilobium hosts. To it he gave the name *Pucciniastrum Abieti-Chamaenerii* because he considered it different from Persoon's *Uredo pustulata*. While his experimental results have been accepted and confirmed, his taxonomic interpretation, as might be expected, is still in dispute. Thus, Sydow (18) agrees with him and, out of hand, refers all of the Pucciniastrum rusts on species of the subgenus Chamaenerion to *P. Abieti-Chamaenerii* Kleb., and all on those of the subgenus Lysimachion to *P. Epilobii* Otth (interpreted by Sydow as *Uredo pustulata* Pers.). Arthur (1) and Hiratsuka (6, 7), on the other side and on no sounder grounds, refer all of both groups to just one species of *Pucciniastrum,* although the former does concede that this may comprise two biological strains or perhaps two varieties. Moreover, Arthur (1) extends the host list to include *Godetia* and *Clarkia,* with the modifying statement that the rust on these hosts "possibly" constitutes "a third variety." There the matter has rested — (a) two described species which may or may not be the same; (b) one life history; (c) proof of some specific host restriction

within the genus *Epilobium;* and (d), according to the point of view, one host list or two host lists, tabulated in either instance without knowledge of the haploid phases and mostly without clarifying cross-inoculation tests.

As a contribution towards an enlarged understanding of the Pucciniastrum-Epilobium rusts, the researches presented in this paper were threefold in purpose — (1) to work out the complete life history of a rust from one selected host of each of the two subgenera of *Epilobium*, that is, one from a Chamaenerion and one from a Lysimachion; (2) to make a complete morphological comparison of these rusts; (3) to compare their biological behavior and the relative susceptibility of their respective hosts as revealed by suitable cross-inoculation experiments. The hosts selected were *Epilobium* (Chamaenerion) *angustifolium* L. and *E.* (Lysimachion) *adenocaulon* Haussk. In designating the corresponding rusts it is convenient to adopt tentatively the nomenclature of Sydow's Monographia Uredinearum, but without any assumption that it is correct or final.

A. THE RUST ON EPILOBIUM (CHAMAENERION) ANGUSTIFOLIUM

Pucciniastrum Abieti-Chamaenerii Kleb. on *Epilobium angustifolium* is very abundant throughout a large part of the northern hemisphere. It is especially common wherever *E. angustifolium* occurs in the neighborhood of certain species of *Abies,* a circumstance explained by the facts that it has its haploid phase on *Abies* and that both kinds of hosts are very susceptible to infection. Incidentally it should be noted that in some instances young plants of *Abies* suffer much damage from the rust. It would make an interesting and perhaps profitable survey to determine the effect of this rust in some localities on the natural reproduction of *Abies.*

Forty years ago or thereabouts, an excellent study of the life history of *P. Abieti-Chamaenerii* was made by Klebahn (9–13). He readily secured infection on *Abies alba* Mill. and then carried the rust back to *E. angustifolium.* He also inoculated *E.* (Lysimachion) *montanum* L., *E. roseum* Schreb., *E. tetragonum* L. and *E. hirsutum* L. with aeciospores and urediospores respectively; but the results were completely negative. Fischer (4) fully confirmed the findings of Klebahn with respect to the alternation of *P. Abieti-Chamaenerii* between *A. alba* and *E. angustifolium.* Tubeuf (19) followed with inoculation experiments in which he used aeciospores naturally occurring on *A. alba.* These he sowed on *E.* (Chamaenerion) *angustifolium, E. Dodonaei* Vill., *E.* (Lysi-

machion) *parviflorum* Schreb. and *E. hirsutum;* infection resulted on the first two only. Bubák (2) also was successful in obtaining infection on *E. angustifolium* by using naturally occurring aeciospores from *A. alba.* In America, Fraser (5) demonstrated that *A. balsamea* (L.) Mill. is a congenial host for *P. Abieti-Chamaenerii* and he made successful reciprocal cultures. Likewise, Weir and Hubert (20–22) secured infection of *A. lasiocarpa* Nutt. after inoculations with telial material from *E. angustifolium;* they were equally successful in culturing back to *E. angustifolium.* Finally, Hiratsuka (6), in Japan, cultured *P. Abieti-Chamaenerii* of *E. angustifolium* origin on *A. Mayriana* Miyabe et Kudô.

Obviously it would be superfluous now merely to confirm again Klebahn's results. But for the purpose of the present comparative research it was essential to obtain both authentic haploid material and detailed experimental data. Accordingly careful, controlled culture work was undertaken. Complete data on the cultures made are compiled in Tables 1 and 2.

I gratefully acknowledge the assistance of Dr. G. D. Darker and Dr. E. H. Moss in making the cultures recorded in Tables 1–4.

TABLE 1

PUCCINIASTRUM ABIETI-CHAMAENERII FROM EPILOBIUM ANGUSTIFOLIUM TO ABIES BALSAMEA

1. *Thirty-seven inoculation experiments* were made under properly controlled conditions. All experiments gave positive results. All controls remained free from infection. Celluloid tubes were used as moist chambers.

2. Inoculations were begun immediately after the unfolding of the new needles. The dates ranged from June 13 to July 4.

3. The telial material used as inoculum was overwintered in net bags out of doors. Just before being used it was placed in a moist chamber and kept there 3 or 4 days, that is, until the teliospores began to germinate.

4. The spermogonia were first observed in from 10 to 14 days after inoculation. *The average was 11.6 days.*

5. The peridermia were first observed in from 15 to 20 days after inoculation. *The average was 17.1 days.*

6. The peridermia usually began to rupture the day following their first appearance.

7. The production of peridermia was practically completed in from 19 to 34 days after inoculation. *The average was 22 days.*

8. The number of infected needles per experiment ranged from 3 to 148 and the percentage of infection from 2 to 75. *The averages were 46 and 25 respectively.*

TABLE 1 (Continued)

9. All infected needles produced spermogonia; but some did not produce peridermia.

10. The number of needles with peridermia varied from 3 to 125. *The average was 40.*

11. The average number of peridermia per needle varied from 22 to 41. *The grand average was 33.*

12. The culture materials, with one exception, are preserved as specimens in the J. H. Faull Herbarium under numbers 8141–8155 and 8515–8535. They are accompanied with the detailed data in tabular form, summaries of which are given above.

TABLE 2

PUCCINIASTRUM ABIETI-CHAMAENERII FROM ABIES BALSAMEA TO EPILOBIUM ANGUSTIFOLIUM

1. *Sixteen inoculation experiments* were made under properly controlled conditions. All experiments gave positive results. All controls remained free from infection.

2. Aeciospores used as inoculum were produced on *Abies balsamea* following inoculations on that host with telial material from *Epilobium angustifolium*, except for a field source of the aeciospores, apparently of *E. angustifolium* origin, in three experiments.

3. Five of the experiments were made on undisturbed plants; eleven were made on detached leaves in Petri dishes.

4. The dates of inoculation ranged from July 5 to July 14.

5. In the experiments on rooted plants the number of inoculated leaves ranged from 4 to 14, *a total of 45 leaves.* All were infected and uredia formed on all but one of them.

6. The uredia were first observed in from 9 to 10 days after inoculation, and these matured in from 11 to 12 days after inoculation.

7. Telia formed in all of the experiments and on a total of at least 19 leaves.

8. Telia were first observed in from 23 to 30 days after inoculation. *The average was 27 days.*

9. In the experiments on detached leaves all were infected and all produced uredia.

10. The uredia were first observed in from 7 to 8 days after inoculation and these matured in from 8 to 9 days after inoculation.

11. The number of uredia per leaf varied from 50 to 219. *The average was 82.*

12. Parallel experiments throughout were made by inoculating *Epilobium adenocaulon.* In no case did infection result from inoculations with the rust of *E. angustifolium* origin.

TABLE 2 (Continued)

13. The culture materials are preserved as specimens in the J. H. Faull Herbarium under numbers 8167, 8221–8224 and 8556 (1–11). They are accompanied with the detailed data in tabular form, summaries of which are given above.

B. THE RUST ON EPILOBIUM (LYSIMACHION) ADENOCAULON

Heretofore there appears to be no published account of the life history of any *Pucciniastrum* originating on an *Epilobium* of the subgenus Lysimachion. The only known pertinent reference of positive value on the subject is a brief statement by Rhodes et al. (16) to the effect that "Bethel (in Mss.) in 1914 obtained uredinia on *Epilobium adenocaulon* from aeciospores from *Abies concolor*."

For the present research, *E. adenocaulon* was chosen because of its abundance in the same region as that in which my experimental material of *E. angustifolium* grew. Moreover, both hosts were everywhere heavily rusted. Relative to the rust on *E. adenocaulon* it has been somewhat of a surprise to learn from the literature that its telia are held to be rare or entirely lacking. Thus Weir and Hubert (21) state that "the fact that this form of the rust" (that is, *P. pustulatum*) "on *E. adenocaulon* produces no telia is evidence of its continuation in the uredinial stage and also explains the absence of a corresponding aecial stage upon Abies." Weir and Hubert are in error on both counts. Out of 11 field collections in my own herbarium all 11 of them carry telia. These come from Alberta, New Brunswick, Ontario, Quebec, Wisconsin and Wyoming. Seven of them were collected in the month of August — two in the first half of the month and one of them as early as August 1. Three were collected in September, the latest on September 14, and one was collected on July 12. Moreover, the telia in many of the collections are conspicuous and often exceedingly abundant on leaves as well as on stems. Likewise telia developed in such of my cultures as were left intact for little more than 30 days. As for the impression that the haploid phase does not occur on *Abies*, that is groundless. *Abies* is highly susceptible to the *Pucciniastrum* on *E. adenocaulon*, as can be inferred from the data embodied in Table 3. Attention is also drawn to the fact that Bethel, as referred to above, apparently found a natural occurrence of this rust on *Abies concolor*.

The rust for my experiments, for convenience designated here by the name *Pucciniastrum Epilobii* Otth apud Sydow, originated in the telial stage on *E. adenocaulon*. Cultures were first made on *Abies balsamea* and then aeciospores thus obtained were sown back on to controlled,

rust-free plants of the original host, *E. adenocaulon*. The data are summarized below in Tables 3 and 4.

TABLE 3

PUCCINIASTRUM EPILOBII FROM EPILOBIUM ADENOCAULON TO ABIES BALSAMEA

1. *Thirty inoculation experiments* were made under properly controlled conditions. All experiments gave positive results. All controls remained free from infection. Celluloid tubes were used as moist chambers.

2. Inoculations were begun immediately after the unfolding of the new needles. The dates ranged from June 9 to July 3.

3. The telial material used as inoculum was overwintered in net bags out of doors. Just before being used it was placed in a moist chamber and kept there 3 or 4 days, that is, until the teliospores began to germinate.

4. The spermogonia were first observed in from 9 to 15 days after inoculation. *The average was 11.1 days.*

5. The peridermia were first observed in from 18 to 29 days after inoculation. *The average was 20.1 days.*

6. The peridermia usually began to rupture the second day following their first appearance.

7. The production of peridermia was practically completed in from 24 to 44 days after inoculation. *The average was 29 days.*

8. The number of infected needles per experiment ranged from 8 to 121 and the percentage of infection from 4 to 57. *The averages were 49 and 24 respectively.*

9. All infected needles produced spermogonia; but some did not produce peridermia.

10. The number of needles with peridermia varied from 2 to 112. *The average was 39.*

11. The average number of peridermia per needle varied from 20 to 37. *The grand average was 27.*

12. The culture materials are preserved as specimens in the J. H. Faull Herbarium under numbers 8156–8157, 8513–8514 and 9585 a-z. They are accompanied with the detailed data in tabular form, summaries of which are given above.

TABLE 4

PUCCINIASTRUM EPILOBII FROM ABIES BALSAMEA TO EPILOBIUM ADENOCAULON

1. *Ten inoculation experiments* were made under properly controlled conditions. All experiments gave positive results. All controls remained free from infection.

2. Aeciospores used as inoculum were produced on *Abies balsamea* fol-

TABLE 4 (Continued)

lowing inoculations on that host with telial material from *Epilobium adenocaulon*.

3. Six of the experiments were made on undisturbed plants; four were made on detached leaves in Petri dishes.

4. The dates of inoculation ranged from July 11 to July 29.

5. In the experiments on rooted plants all inoculated leaves became infected and all bore uredia.

6. The uredia were first observed 7 to 11 days after inoculation. *The average was 8.7 days.* These matured in 9 to 12 days after inoculation. *The average was 9.7 days.*

7. Telia formed within 34 days after inoculation.

8. In the experiments on detached leaves all were infected and all produced uredia.

9. The uredia were first observed in from 9 to 10 days after inoculation, and these matured in from 10 to 11 days after inoculation.

10. The number of uredia per leaf on the rooted plants varied from 63 to 800. *The average was 214.* The number of uredia on the detached leaves varied from 52 to 230. *The average was 165.*

11. Parallel experiments throughout were made by inoculating *Epilobium angustifolium*. In no case did infection result from inoculations with the rust of *E. adenocaulon* origin.

12. The culture materials are preserved as specimens in the J. H. Faull Herbarium under numbers 8220, 8557 (1–5) and 9595 (1–4). They are accompanied with the detailed data in tabular form, summaries of which are given above.

C. OBSERVATIONS ON BIOLOGY AND MORPHOLOGY OF THE TWO RUSTS

It is plain from the data recorded above (Tables 1 and 3) that the Pucciniastrum rusts on *Epilobium angustifolium* and *E. adenocaulon*, respectively, can readily and abundantly infect the new foliage of *Abies balsamea*. Similarly, they can as easily be carried back from *A. balsamea* to their original Epilobium hosts. But all attempts to establish the rust of *E. angustifolium* origin on *E. adenocaulon*, whether by means of aeciospores or urediospores, completely failed. So, too, it was impossible to bring about infection of *E. angustifolium* with the rust of *E. adenocaulon* origin. In other words, these rusts are physiologically differentiated from one another with respect to their infective capacity. Along with this biological specialization there also exist, as we shall now see, certain differences in habit and in form.

Since comparisons of the growth habits of rust fungi are not taxo-

nomically usable unless the environmental growth factors have been identical, the observations noted here are perforce restricted to the haploid phase, that is, to the phenomena manifested on the common host, *Abies balsamea*. Obviously comparisons are pointless that are based on the diploid phase occurring on separate specific hosts, such for example as those advanced by Sydow (18) in justification of his recognition of *Pucciniastrum Abieti-Chamaenerii* and *P. Epilobii* as distinct species. With respect to the rusts of the present research, the differences observed on *Abies balsamea* may be summarized as follows. (1) The rust from *Epilobium angustifolium* produces peridermia within an average of 17 days after inoculation; the rust from *E. adenocaulon* requires an average of 20 days. (2) The average time for approximately complete development of its crop of peridermia is 22 days in the case of the first and 29 days in the case of the second. (3) The average numbers of peridermia per infected needle are 33 and 27 respectively. (4) In general the *E. angustifolium* rust occurs more frequently and more severely on the needles of the upper part of the current season's growth; the *E. adenocaulon* rust is localized more often on the lower part of the current season's growth.

Turning next to comparisons of form, it has been found that some differences exist between the *E. angustifolium* and the *E. adenocaulon* rusts. The spermogonia were studied comparatively by Hunter (8). The materials examined by her were taken from the cultures reported above. They were suitably fixed when fresh, embedded in paraffin and sectioned. Hunter concluded that the spermogonia of the respective forms cannot be distinguished from one another with certainty. The aecia, on the other hand, do show some differences. As a rule those of the rust originating on *E. angustifolium* are narrower, varying from 0.012 to 0.025 mm. in diameter; the peridium is fragile and soon breaks down; the aeciospores average about 15 × 19 μ and they are very finely warted. The peridermia of the rust originating on *E. adenocaulon* vary from 0.02 to 0.04 mm. in diameter; the peridium is quite persistent; the spores average about 14 × 18 μ and are subcoarsely warted. As for the diploid phase, the teliospores of the two rusts show much the same range of organization, size and form. But the urediospores of the *E. angustifolium* rust are broader than those of the *E. adenocaulon* rust. They average about 16 × 19 μ in size as compared with about 14 × 19 μ for the latter. The walls, too, of the peridial cells are quite distinctive. They measure up to 1.5 μ in thickness for the *E. angustifolium* rust and up to 2.5 μ for the *E. adenocaulon* rust.

With these physiological and morphological data in hand, we can

now deal with the taxonomy of the Pucciniastrum rusts on *Epilobium angustifolium* and *E. adenocaulon* on surer grounds than has heretofore been possible. Unquestionably they should be nomenclatorially differentiated, whether as forms or varieties with trinomial designations, or as species with binomials. The latter is certainly the simpler procedure and in practice the more expedient at present. For my own part I am inclined to accept the Sydow point of view, as also that of Klebahn and certain others, in recognizing two distinct species of *Pucciniastrum* on *Epilobium*, and to tentatively refer the one species to Chamaenerion hosts and the other to Lysimachion hosts. Just what names should be adopted, however, is another matter.

As for the Lysimachion rust, Sydow chose the name *Pucciniastrum Epilobii* Otth; but he did so apologetically because it seemed probable that Otth's material was the rust on *E. angustifolium*. Of course DeCandolle (3) had long since coined the name *Uredo Epilobii* for the Pucciniastrum rust on the Lysimachion host *E. tetragonum*. But doubtless Sydow, in accordance with his own interpretation of the International Rules of Nomenclature, did not feel bound to accept DeCandolle's specific name because DeCandolle, in connection therewith, made no mention of teliospores. But why not accept the name *Pucciniastrum pustulatum* (Pers.) Dietel in part? Persoon's name likewise referred to a rust on a Lysimachion host (*E. montanum*). True he, too, made no mention of teliospores, but the specific name would seem to have been validated by Dietel, quite in accord with Sydow's legalistic conceptions, even though Dietel did extend its applicability to the rust on Chamaenerion hosts.

As for the Chamaenerion rust, the nomenclatorial tangle is perhaps even more involved. But as the specific names referred to above were based, though fortuitously so, on Lysimachion host material, they can well be dropped from consideration. Actually Rostrup (17) was the first to claim that the Chamaenerion rust was not identical with the Lysimachion rust. Accordingly he gave to it the specific name "Chamaenerii," but without description. That brings us to Klebahn (13). From his experimental results he reached the same conclusion as Rostrup and described the Chamaenerion rust under the name *Pucciniastrum Abieti-Chamaenerii*. Sydow accepted Klebahn's findings and this choice appears to be entirely justifiable.

SUMMARY

1. Approximately 40 species of *Epilobium* (Chamaenerion and Lysimachion) have at one time or another been listed as hosts of Puccinias-

trum rusts. Investigators in Europe, America and Japan have demonstrated that the form on *E. angustifolium* passes to *Abies*. It also passes to two other species of Chamaenerion. Inoculations on several species of Lysimachion gave negative results. No other significant experimental work has been done. In consequence, taxonomic conclusions have been clouded and certain economic considerations subject to surmise.

2. This paper records for the first time the complete life history of a *Pucciniastrum* from a Lysimachion host (*E. adenocaulon*). It develops its haploid phase on *Abies balsamea*.

3. Tests made at the same time show that the *E. angustifolium* rust does not cause infection of *E. adenocaulon;* nor does the *E. adenocaulon* rust cause infection of *E. angustifolium*.

4. This specialization in infective capacity is accompanied by differences in habit on the common host *Abies balsamea* and by morphological distinctions for both the aecia and the uredia of the respective rusts.

5. These rusts, therefore, should be nomenclatorially differentiated, whether as forms or varieties, or as distinct species. Specific recognition is preferable. For the rust on *E. angustifolium*, the name *Pucciniastrum Abieti-Chamaenerii* Kleb. seems to be acceptable, and the name *P. pustulatum* (Pers.) Diet. in part, for the one on *E. adenocaulon*. Further culture work may show that the former is restricted to Chamaenerion hosts and the latter to Lysimachion hosts.

6. Field experience and controlled cultures prove that *Abies balsamea* is highly susceptible to these rusts. They often cause severe damage to young trees of *A. balsamea* where the corresponding rusted Epilobium hosts occur.

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